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Temperature dependence of the relationship between pCO_2 and dissolved organic carbon in lakes

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Abstract. The relationship between the partial pressure of carbon dioxide (pCO_2) and dissolved organic carbon (DOC) concentration in Brazilian lakes, encompassing 225 samples across a wide latitudinal range in the tropics, was tested. Unlike the positive relationship reported for lake waters, which was largely based on temperate lakes, we found no significant relationship for low-latitude lakes (< 33°), despite very broad ranges in both pCO_2 and DOC levels. These results suggest substantial differences in the carbon cycling of low-latitude lakes, which must be considered when upscaling limnetic carbon cycling to global scales.

1 Introduction

Lakes cover less than 2 % of the continent's surface (Downing et al., 2006; McDonald et al., 2012) but play a significant role in the global carbon (C) cycle (Cole et al., 1994, 2007; Tranvik et al., 2009), contributing significantly to C burial and emissions to the atmosphere (Cole et al., 2007; Downing et al., 2008; Tranvik et al., 2009). Dissolved organic carbon (DOC) represents a major C pool in lakes, with both autochthonous and allochthonous contributions (Duarte and Prairie, 2005; Cole et al., 2007; Prairie, 2008; Tranvik et al., 2009), supporting heterotrophy (Sobek et al., 2007) and affecting key biological and physicochemical processes involved in C cycling (Steinberg et al., 2006). Large inputs of terrestrial organic C and its subsequent mineralization have been suggested to be a major driver of CO_2 supersaturation commonly encountered in lakes (Duarte and Prairie, 2005; Cole et al., 2007; Prairie, 2008; Marotta et al., 2009).

The mechanistic connection between DOC and heterotrophic CO_2 production is believed to underpin the significant positive relationship between pCO_2 and DOC reported in comparative analyses (Houle et al., 1995; Sobek et al., 2005; Larsen et al., 2012). However, recent analyses have revealed that the relationship between pCO_2 and DOC in lake waters is regionally variable and not universal (Lapiere and del Giorgio, 2012). Hence, the relationship between pCO_2 and DOC reported in comparative analyses, based on data sets dominated by temperate and high-latitude lakes (> 33°), may not be extrapolated for all types of lakes, mainly because the tropical low-latitude lakes (< 33°) are generally underrepresented in global data sets (Raymond et al., 2013).

One priority of comparative studies is the latitudinal variance, where lake temperature, ice cover and mixing regime will differ and these climatically driven processes, in turn, should strongly influence organic carbon cycling (Hanson et al., 2015). At low latitudes, warm conditions over the whole year may increase the metabolic rates involved in the C cycling in terrestrial (Ometto et al., 2005) and aquatic (Marotta et al., 2009, 2010) ecosystems on an annual basis compared to the high-latitude lakes. High temperatures affect heterotrophic activity and the associated mineralization rates of organic matter in soils (Davidson and Janssens, 2006), waters (López-Urrutia and Morán, 2007; Wohlers et al., 2008; Regaudie-de-Gioux and Duarte, 2012) and aquatic sediments (Wadham et al., 2012; Gudasz et al., 2010; Marotta et al., 2014). Enhanced heterotrophic activity in warm ecosystems would support high aquatic CO_2 production and subsidize high CO_2 evasion from global lake water to the atmosphere.

The largest previous comparative analysis already published in the literature for global lake waters (Sobek et al., 2005) reported a significant positive relationship between DOC and pCO_2 and a non-significant variation of pCO_2 among lakes with changing temperature. However, both analyses were characterized by a paucity of low-latitude data. A strong positive relationship between temperature and pCO_2 was observed when subtropical and tropical ecosystems were included in the data set (Marotta et al., 2009), likely caused by the potential increase in metabolic rates under warmer conditions (Brown et al., 2004; López-Urrutia et al., 2006). Hence, the relationship between lake pCO_2 and DOC could also be temperature-dependent and, therefore, may differ between temperate and tropical lakes. The extensive low-latitude territory of Brazil, which has a high density of lakes and ponds (Downing et al., 2006), is appropriate to examine general patterns in the tropics (e.g., Marotta et al., 2009; Kosten et al., 2010). Here, we test the applicability of the relationship between pCO_2 and DOC using inputs derived from a high-latitude data set (Sobek et al., 2005) with added tropical and subtropical data of low-latitude lakes from Brazil.

2 Methods

2.1 Study area and lakes

Brazil extends from 5°16′20″ N to 33°44′42″ S, covering an area of approximately 8 547 000 km^2, constituting half of South America, and it encompasses a high diversity of low-latitude landscapes (Ab'Saber, 2003) that are predominantly located within tropical latitudes. We conducted a survey of pH, alkalinity and DOC between 2003 and 2011 in surface waters of 166 permanent lakes from 0 to 33° of south latitude across Brazil (Fig. 1), yielding a total of 225 water samples. The lakes were sampled in representative biomes of Brazil: (1) the Amazonia forest (Amazonia biome, $n = 65$), (2) the Pantanal floodplain (Pantanal biome, $n = 29$) and (3) the tropical (< 24° of latitude) and (4) subtropical (> 24° and < 33° of south latitude) coasts, both in the Atlantic Forest biome ($n = 35$ and $n = 37$ lakes, respectively; Fig. 1). These biomes follow the classification of the Brazilian Institute of Geography and Statistics for biomes (IBGE 2004, ftp://geoftp.ibge.gov.br/mapas_tematicos/mapas_murais/biomas.pdf). Our data set encompasses a broad inter-lake heterogeneity ($n = 166$) for pH, alkalinity and DOC, simultaneously sampled among Brazilian biomes and along the latitudinal gradient, independent of the year's season.

The Amazonian Forest biome is formed by the most extensive hydrographic network on the globe – the Amazon River basin – which occupies a total area of approximately 6.11 million km^2 from its headwaters in the Peruvian Andes to its mouth in the Atlantic Ocean (ANA – www.ana.gov.br). The Amazon Forest is the Brazilian biome with the highest mean annual precipitation (approximately 2200 mm) and has warm mean air temperatures, approximately 25 °C, high cloud coverage and high humidity with low fluctuations over the whole year (Chambers, 1999). We sampled a wide variety of lakes, characteristic of different areas of the Amazonian Forest, encompassing "clear" (low DOC and suspended solids), "white" (low DOC and high suspended solids) and "dark" (high DOC and low suspended solids) lakes.

The Pantanal floodplain is the world's largest tropical freshwater wetland, extending across an area of approximately 150 000 km^2 between 16 and 20° S and 58 and 55° W (Por, 1995). The annual average temperature and precipitation are approximately 22 °C and 1000 mm, respectively (Mariot et al., 2007), with a strong seasonality and subsequent variation in the flooded area (Junk and Nunes da Cunha, 2005). The high-water period occurs during the rainy summer (usually from September to December), and low waters typically occur during the dry winter (from March to July; Hamilton et al., 2002).

The Atlantic Forest biome extends along a broad latitudinal belt, between 5 and 30° S from the subtropics to tropics and a narrow longitudinal section between 55 and 56° W, and occupies an area of 1.11 million km^2 along the Brazilian coast (IBGE; www.ibge.gov.br). This biome is characterized by numerous shallow coastal lakes, receiving high inputs of refractory organic matter (Farjalla et al., 2009) derived from the typical open xerophytic vegetation on sandy soils, where water retention is low (Scarano, 2002). The mean air temperatures vary from 27 °C in winter to 30 °C in summer at the tropical coast (< 24° of latitude; Chellappa et al., 2009) and from 17 and 20 °C at the subtropical coast (> 24° of latitude; Waechter, 1998). The mean annual precipitation reaches 1164 mm (Henriques et al., 1986)

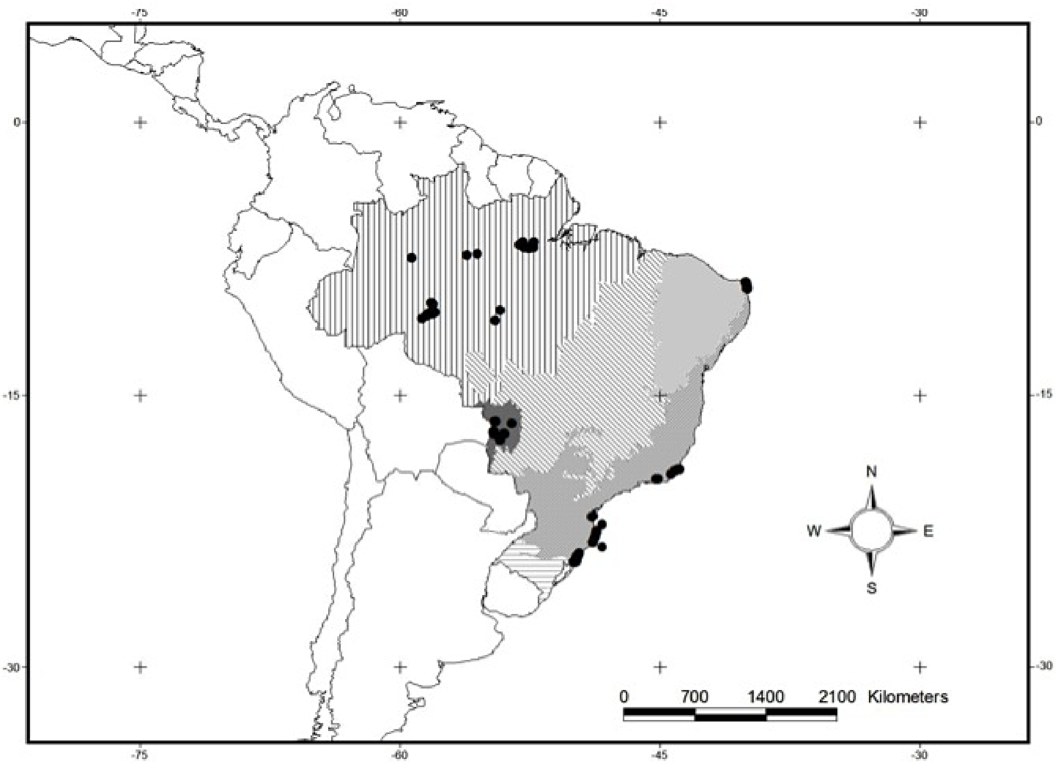

Figure 1. Geographic location of Brazilian lakes sampled in different biomes (IBGE 2004, available at ftp://geoftp.ibge.gov.br/mapas_tematicos/mapas_murais/biomas.pdf): Amazonia forest (vertical lines), Pantanal floodplain (dark gray) and Atlantic Forest (gray; tropical and subtropical coastal lakes).

and 1700 mm (Waechter, 1998) in the tropical and subtropical Brazilian coast, respectively. This biome is also characterized by strong seasonality, with rainy summers and dry winters (Chellappa et al., 2009).

2.2 Sampling design and analytical methods

Our sampling design encompassed the most representative Brazilian biomes from tropical and subtropical coastal areas to tropical and subtropical forests (Amazon and Atlantic Forest) and inland wetlands (Pantanal), with the intra-lake heterogeneity and seasonal fluctuations randomly assessed and further integrated by means of each ecosystem. To analyze the relationship between $p\mathrm{CO_2}$ and DOC in tropical lake waters, we joined data on 194 lakes ($< 33°$ of latitude) with both variables sampled at the same time, including 166 data samples from our own survey and 28 from the literature compilation (Table S1 in the Supplement). The values reported here, gathered in an opportunistic manner, represent daily averages ($N = 4$ or 5 samples) for a given year's season or/and one sampling time over different seasons, which were also both integrated by means of each lake. To test the global importance of the relationship between $p\mathrm{CO_2}$ and DOC, we added our low-latitude data (225) to the Sobek et al. (2005) data set (4902 lakes) as this data set had a paucity of tropical ecosystem data (148 tropical lakes, but only one with $p\mathrm{CO_2}$ and DOC sampled at the same time).

pH, salinity and temperature were measured in situ. pH was determined using a pH meter (Digimed – DM2) with reference standards certified by Mettler Toledo (4.00 ± 0.01 and 7.00 ± 0.01 units) before each sampling hour. Temperature and salinity were measured using a thermosalinometer (Mettler Toledo – SevenGo™ SG3) coupled to a probe in Lab 737 previously calibrated with 0.01 M KCl. Surface lake water was collected for total alkalinity and DOC analyses, taking care to avoid bubbles at approximately 0.5 m of depth using a 1 L Van Dorn bottle. Total alkalinity (TA) was determined in the field by the Gran's titration method with 0.0125 M HCl immediately after sampling (Stumm and Morgan, 1996). Water samples for DOC were pre-filtered (0.7 µm, Whatman GF/F) and preserved by acidification with 85 % $\mathrm{H_3PO_4}$ to reach a pH < 2.0 in sealed glass vials (Spyres et al., 2000). In the lab, DOC was determined by high-temperature catalytic oxidation using a TOC-5000 Shimadzu Analyzer; quality control was checked with a calibration curve made with potassium hydrogen phthalate before each sample battery analysis. $p\mathrm{CO_2}$ concentrations in surface waters were calculated from pH and alkalinity following Weiss (1974), after corrections for temperature, altitude and ionic strength according to Cole et al. (1994).

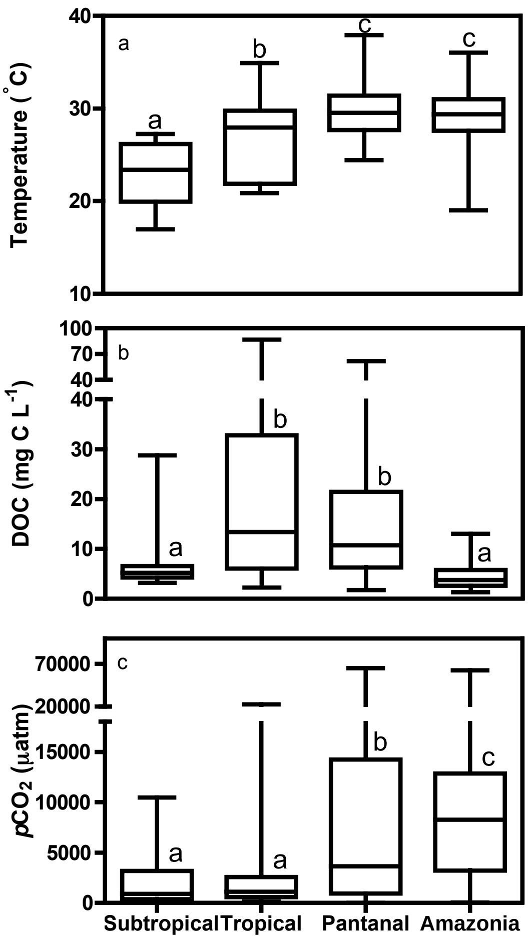

Figure 2. Values of **(a)** temperature (°C), **(b)** DOC concentrations ($mg\,C\,L^{-1}$) and **(c)** pCO_2 concentration (µatm) of Brazilian lakes sampled from different biomes, as defined by subtropical coastal lakes ($n = 37$), tropical coastal lake ($n = 63$), Pantanal floodplain ($n = 58$) and Amazonia forest ($n = 67$). The line depicts the median. The boxes show the quartiles, and the whiskers mark the 10th and 90th percentiles. Different lowercase letters near the box plot indicate significant statistic differences between the groups (Kruskall–Wallis followed by Dunn's multiple comparison post hoc test, $p < 0.05$).

In order to address the potential contribution of DOC to TA, which is especially important in DOC-enriched acid freshwaters, we used the data set from Abril et al. (2015) to correct pCO_2 values calculated from pH and TA after the corrections for temperature, altitude and ionic strength (Cole et al., 1994). Full details on fitted regression equations to correct pCO_2 in function of the DOC and pH are described in the Supplement (Fig. S3).

2.3 Statistical analyses

The variables pCO_2 and DOC did not meet the assumptions of parametric tests even after logarithmic transformations (Zar, 1996) as the data were not normally distributed

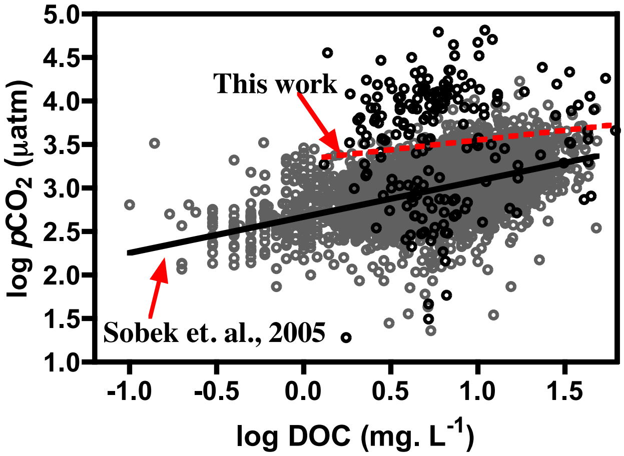

Figure 3. Comparisons of pCO_2 against DOC concentrations for lakes from this study (black circles) and from Sobek et al. (2005; gray circles). Each point in the plot represents one measurement. The dashed line represents the linear regression for all Brazilian data points (not significant; $p > 0.05$), and the solid line represents the linear regression from Sobek et al. (2005; $p < 0.05$, $R^2 = 0.26$, $\log pCO_2\ (\mu atm) = 2.67 + 0.414 \log DOC$; $mg\,C\,L^{-1}$).

(Kolmogorov–Smirnov, $p < 0.05$) and the variances were heterogeneous (Bartlett, $p > 0.05$). Therefore, we used medians and nonparametric tests to compare these variables among biomes (Kruskall–Wallis followed by Dunn's multiple comparison post hoc test, $p < 0.05$). The linear regression equations were fitted to compare our results with those of previous studies from Sobek et al. (2005). Statistical analyses were performed using the software Graphpad Prism version 4.0 for Macintosh (GraphPad Software, San Diego, CA).

3 Results

The lake waters surveyed were warm across all biomes (median 25–75 %, interquartile range = 27.5 °C, 25.2–30.1) but colder in subtropical coastal lakes (23.4 °C, 20.0–26.2) than in Pantanal and Amazonian lakes (29.5 °C, 27.7–31.4 and 29.4 °C, 27.6–31.0, respectively; Dunn's test, $p < 0.05$, Fig. 2a). DOC concentrations were consistently high (6.3 $mg\,C\,L^{-1}$, 4.3–11.9) for all Brazilian biomes but significant lower in the Amazonian Forest (3.8 $mg\,C\,L^{-1}$, 2.7–5.8) than in the tropical coast (13.4 $mg\,C\,L^{-1}$, 6.1–32.8; Fig. 2b; Dunn's test, $p < 0.05$). Most lakes (approximately 83 % of raw data) showed surface waters supersaturated in CO_2 relative to the atmospheric equilibrium (pCO_2 in atmospheric equilibrium is 400.83 µatm, 2015 annual mean; data available in www.esrl.noaa.gov/gmd/ccgg/trends), with much higher pCO_2 values in Amazonian lakes (7956 µatm, 3033–11 346) than in subtropical coastal lakes (900 µatm, 391.3–3212; Fig. 2c; Dunn's test, $p < 0.05$).

The pCO_2 in the surface waters of Brazilian lakes was independent of DOC concentrations (linear regression for raw data, $p > 0.05$, Fig. 3). The same absence of positive significance pattern was found in comparison with corrected data. A negative (linear regression, $p < 0.05$, $R^2 = 0.03$, $n = 194$, $pCO_2 = -98.76\ (\pm 39.92) \times \text{DOC} + 6529\ (\pm 641.1)$) or non-significant (linear regression, $p > 0.05$) DOC–pCO_2 relationship for tropical lakes ($N = 194$, DOC- and pH-corrected data, respectively (Fig. S3a and c)) contrasted with a significant positive relationship for those at other latitudes ($N = 4433$; linear regression, $p < 0.05$, $R^2 = 0.20$, $pCO_2 = 64.43\ (\pm 2.04) \times \text{DOC} + 625.1\ (\pm 20.87)$ and $R^2 = 0.12$, $pCO_2 = 45.70\ (\pm 1.84) \times \text{DOC} + 623.7\ (\pm 18.83)$) for DOC-corrected data and pH-corrected data, respectively (Fig. S3b and d, full details on corrections in the Supplement). The range of pCO_2 for a similar DOC range in Brazilian lakes was larger than that reported by Sobek et al. (2005) for the data set dominated by high-latitude cold lakes, despite the number of lakes in their data set being much larger (more details in the Supplement, Fig. S3).

4 Discussion

The Brazilian lakes sampled here were characterized by a prevalence of CO_2 supersaturation, consistent with general trends previously reported for global lakes (e.g., Raymond et al., 2013; Cole et al., 1994, 2007), including those at tropical latitudes (Marotta et al., 2009). The very high pCO_2 levels observed here, with a median of 900 and 8300 µatm for subtropical and Amazon lake waters, respectively, are consistent with those reported previously for the Amazon River and tributaries (2000–12 000 µatm; Richey et al., 2002), Amazon floodplain lakes (3000–4898 µatm; Rudorff et al., 2012), Pantanal lakes and wetlands (2732–10 620 µatm; Hamilton et al., 1995), and coastal lakes (768–9866 µatm; Kosten et al., 2010; 361–20 037 µatm; Marotta et al., 2010) and for global values for tropical lakes (1255–35 278 µatm; Marotta et al., 2009), reservoirs (1840 µatm; Aufdenkampe et al., 2011) and wetlands (3080–6170 µatm; Aufdenkampe et al., 2011).

The non-significant or weakly negative relationship (Fig. S3) between DOC and pCO_2 reported here for warm low-latitude lakes contrasted with significant positive relationships derived from previous data sets dominated by high-latitude lakes (Houle, 1995; Prairie, 2002; Jonsson et al., 2003; Sobek et al., 2005; Roehm et al., 2009; Lapiere and del Giorgio, 2012; Larsen et al., 2012). The results presented show that warm low-latitude lakes range widely in pCO_2, reaching very high and low values, but tend to have comparatively more uniform DOC concentrations (Fig. 3). More intense metabolic processes that uptake and release CO_2 in lake waters, autotrophy and heterotrophy, respectively, could determine an enhanced variability in lake pCO_2 with decreasing latitude (Marotta et al., 2009).

In this way, the inclusion of warm tropical data in our study revealed novel increases in the variability of the DOC–pCO_2 relationship in lakes over the latitudinal gradient. One explanation for this pattern is that even similar DOC concentrations, representing the total pool of DOC, may show different mixtures between origins from aquatic primary producers and terrestrial sources (Kritzberg et al., 2006). The autochthonous DOC (i.e., produced in the lake) is related to the net CO_2 uptake (Staehr and Sand Jansen, 2007), while the allochthonous DOC (i.e., produced in the catchment) is a resource to the net CO_2 release in lake waters (Sobek et al., 2007). The increased DOC release from aquatic primary producers into waters under tropical conditions, especially warmer annual conditions and higher solar incidence, can offset any positive relationship between pCO_2 and the terrestrial DOC that causes the net aquatic heterotrophy to subsidize (Marotta et al., 2010, 2012). This contributes to the explanation of non-significant relationships reported here (Fig. 3), suggesting a temperature dependence of the DOC–pCO_2 relationship in global lakes.

In conclusion, the finding that pCO_2 does not increase with DOC concentration in Brazilian tropical lakes rejects the hypothesis that DOC serves as a universal predictor for pCO_2 in lake waters (Larsen et al., 2012). Even discounting a possible artifact of the method that could be causing an overestimation in the values of pCO_2 or considering the contribution of organic acids to the alkalinity, the pattern of no relationship between DOC and pCO_2 in the tropical lakes was strongly confirmed (Fig. S3). Therefore, our results, contributing to the filling of a gap in the literature of tropical studies, suggest potentially important latitudinal differences for depositional aquatic environments, whose causes still need to be better addressed to improve accuracy of global C cycle models.

The Supplement related to this article is available online at doi:10.5194/bg-13-865-2016-supplement.

Author contributions. All authors contributed to the study design, data interpretation and preparation or refinement of the manuscript. L. Pinho and H. Marotta performed the sampling and sample analyses.

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